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Research Article

Recent changes in tropical-dry-forest connectivity within the Balsas Basin Biogeographic Province: potential effects on endemic-bird distributions

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Abstract

Maintaining landscape connectivity is a conservation priority for biodiversity as it may mitigate the adverse effects of forest degradation, fragmentation, and climate change by facilitating species dispersal. Despite their importance for biodiversity conservation, Mexican tropical dry forests (TDFs) face high fragmentation rates due to anthropogenic activities. In this study, we analyzed the connectivity dynamics of TDFs in the Balsas Basin Biogeographic Province (BBBP) between 2013 and 2018, focusing on old-growth and secondary TDF covers, including Protected Areas and Important Bird Areas. We evaluated the effects of connectivity loss and gain on the distribution areas of 30 endemic bird species with ecological associations with TDFs in the BBBP. We found expansion in TDFs accounting for a total increase of 227,905 ha due to secondary forest increase (12%). In contrast, old-growth forests experienced a reduction of 66,576 ha in the study area (8%). We also found a decrease in areas with high and very-high connectivity, coupled with an increase in low connectivity, except for TDFs inside Protected Areas, which increased by 3,000 ha, leading to higher connectivity. There was an increase in total forest cover in 27 species' potential distribution, highlighting the possible role of secondary forests in promoting connectivity between old-growth forest patches. Our results reveal the complex dynamics between forest types, connectivity, and bird-species distributions. Despite an overall increase in forested areas, most TDFs continue to have low connectivity, likely impacting biodiversity, particularly for species that rely on highly conserved ecosystems. This study underscores the importance of integrated conservation strategies considering connectivity, forest recovery, and the dynamics of species-ecosystem interactions.

Key words: conservation priorities, important bird areas, old-grow forests, protected areas, secondary forests

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Introduction

Natural forests face severe threats due to degradation, destruction, and fragmentation, significantly impacting biodiversity worldwide (Wilson 1992; Sala et al. 2000; Betts et al. 2017). Such activities lead to reduced habitat availability, increased isolation of forest patches, and higher vulnerability to alien-species invasion, edge effects, and further degradation (Wilcove et al. 1998; Fahrig 2003; Hulme 2009; Bellard et al. 2022). The primary drivers of forest loss are land-use and land-cover change, with tropical regions accounting for nearly 95% of global deforestation (Newbold et al. 2015; Curtis et al. 2018). The consequences of habitat loss affect all ecosystems, especially regarding reduced landscape connectivity, which has far-reaching implications at both local and regional scales.

Connectivity loss is a critical problem affecting biodiversity, as it hinders species' long-distance movements, making it difficult for them to survive in the face of anthropogenic pressures (Krosby et al. 2010; Damschen et al. 2019). Furthermore, conserving landscape connectivity is crucial for mitigating some of the adverse effects of fragmentation and climate change (Taylor et al. 1993; Correa Ayram et al. 2016; Zanin et al. 2016) by facilitating the colonization of available patches and enhancing gene flow among populations (Whitlock et al. 2000; Haddad et al. 2003, 2015). Changes in spatio-temporal land-use and land-cover patterns can significantly reshape the quantity and quality of available habitats for species, profoundly influencing ecological processes, species movements, and patterns of species richness and abundance (Lindborg and Eriksson 2004; Rocha et al. 2018). This intricate interplay of spatial and temporal connectivity creates a dynamic matrix that shapes ecosystems and influences species distributions (Auffret et al. 2015). Therefore, understanding recent connectivity patterns and their effects on species ranges is essential to comprehend ecological responses to fragmentation caused by climate or land-use and land-cover change, and to implement practical biodiversity conservation actions tailored to species' needs (Metzger et al. 2009; Thompson et al. 2017).

Tropical dry forests (TDFs) rank among the world's most endangered ecosystems, having lost nearly 80% of their original cover (Trejo and Dirzo 2000; Miles et al. 2006; Sánchez-Azofeifa et al. 2014). Recent estimates indicate that up to 85% of the remaining TDFs in the Americas face potential risk (Ferrer-Paris et al. 2019). TDFs occupy approximately 17% of Mexican territory, and their geographic isolation classifies them as ecological islands, nurturing distinct floral and faunal groups, including 24% of México's bird-species richness (Rzedowski 1991; Ceballos and García 1995; Dirzo et al. 2011; Navarro-Sigüenza et al. 2014). The Balsas Basin Biogeographic Province (BBBP) is characterized by a unique combination of climatic, ecological, and biotic factors that have influenced the evolution and distribution of its biota (Morrone 2014). It represents the only interior depression in México with tropical vegetation, making it a remarkable ecosystem (Fernández-Nava et al. 1998). However, human activities in this region have transformed many old-growth forests into secondary ones, leading to a complex landscape of degraded and recovering forests (Sánchez-Colón et al. 2009) that result in a mix of vegetation types that originate from different stages of ecological succession (INEGI

2015, FAO 2020a). Despite the dominance of secondary forests, their proximity to old-growth forests highlights their potential as pathways for species colonization (Gray et al. 2007; Mayhew et al. 2019). Secondary forests, particularly those with a developed tree and shrub canopy, might represent an essential habitat for resident and endemic bird species (Ramírez-Albores 2006), acting as corridors and stepping stones between old-growth forests, which host a wide variety of specialist species (Wright and Muller-Landau 2006; Chazdon et al. 2009; Acevedo et al. 2023).

The BBBP holds eight Protected Areas (PAs; CONANP 2022) and numerous Important Bird Areas (IBAs; Arizmendi and Márquez 2000; Devenish et al. 2009), highlighting its significance for conservation efforts. International agendas, such as the Kunming-Montreal Global Biodiversity Framework, emphasize the urgency of maintaining ecological connectivity (IPBES 2019), and the Convention on Biological Diversity (CBD 2020) urges increases in PA coverage worldwide (Vimal et al. 2021). However, the ongoing changes in land use and cover jeopardize the connectedness of PAs, threatening their ecological integrity and the species they harbor. Therefore, a detailed connectivity analysis is vital to assess conservation efforts and guide effective management strategies to safeguard this biodiverse and ecologically crucial ecosystem (Crooks and Sanjayan 2006; Rodrigues and Cazalis 2020). The goal of this study is to analyze recent connectivity dynamics between 2013 and 2018 across old-growth and secondary TDFs of the BBBP, including PAs and IBAs. This analysis aimed to shed light on the potential effects of these dynamics on the distribution of diverse Mexican endemic bird species with ecological affinity to the TDFs. It provides insights into how these dynamics impact the distribution of endemic bird species, therefore contributing to understanding the conservation needs in an ecologically sensitive region.

Methods

Study area

Located in the states of Guerrero, Jalisco, México, Michoacán, Morelos, Oaxaca, and Puebla, the Balsas Basin Biogeographic Province (BBBP) covers nearly 7,640,000 ha (Fig. 1; Morrone 2014; Morrone et al. 2017). The BBBP is a depression in the interior of México that descends from a plateau that reaches up to 1,000 meters above sea level (m a.s.l.), with some scattered peaks at 2,000 m in the north to 200 m in the extreme west (Dinerstein et al. 2017). The BBBP is delimited by the Trans-Mexican Volcanic Belt and the Sierra Madre del Sur, which places it on the border of two mountain complexes of the Mexican Transition Zone in the Neotropical region (Halffter 1976; Halffter and Morrone 2017).

The BBBP remains as an important area covered by tropical dry forests (TDFs) (Rzedowski 2006; Dirzo et al. 2011). TDFs are primarily dominated by relatively short trees that shed their entire foliage during dry seasons (Miranda and Hernández-X 1963). This is due to highly seasonal characteristics, which include a well-defined rainy season (500 – 1,500 mm/yr), followed by a dry season with five to eight months of continuous drought (Jaramillo et al. 2011).

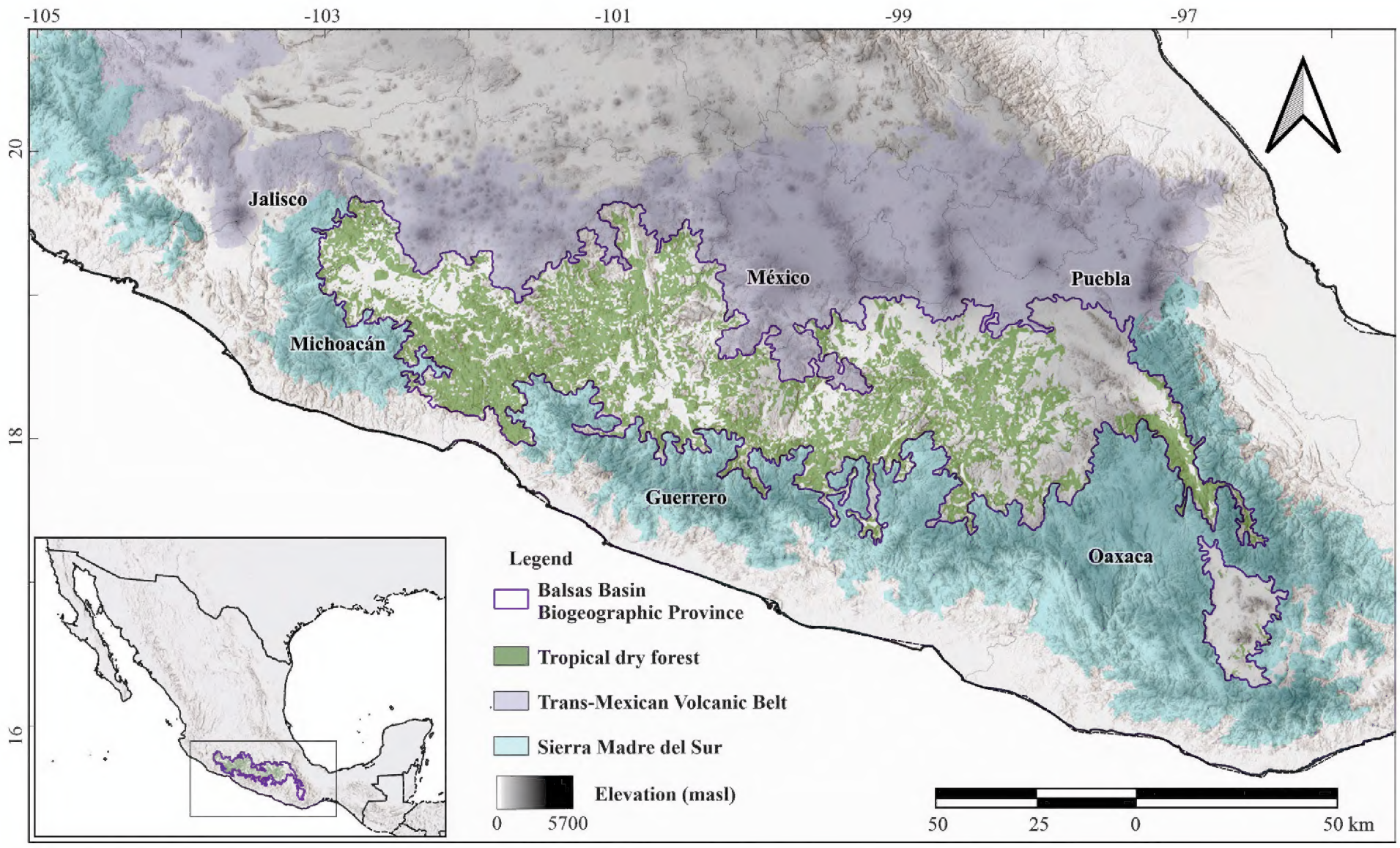


Figure 1. Location of the Balsas Basin Biogeographic Province in México, showing the two adjacent provinces Trans-Mexican Volcanic Belt (light purple), and Sierra Madre del Sur (light blue); the more intense colors (gray scale) represent the higher altitudes.

Species distribution modeling

The selection of avian species for this study was based on the following criteria: 1) species endemic to México (Navarro-Sigüenza and Peterson 2004; Berlanga et al. 2020), 2) species whose distribution overlapped entirely or partially the Balsas Basin Biogeographic Province, 3) species reported as ecologically associated with the TDFs (Stotz et al. 1996; Vázquez-Reyes et al. 2017, 2018) (Suppl. material 1), and 4) species with more than 20 occurrences. Although all selected species occur within TDFs, they are not necessarily exclusive to this vegetation type (Table 1). Their presence in TDFs ranges from preferential to incidental, as they inhabit other vegetation types (Suppl. material 1). From the resulting list, we selected 95% of species (30 species), including a wide range of feeding guilds, forest dependency, and specialization within TDFs, from species that predominantly live in these forests and those that use several other ecosystems (Stotz et al. 1996; Pineda-Diez de Bonilla et al. 2012; Billerman et al. 2022).

To produce the Species Distribution Models (SDMs), we used the Maximum Entropy (MaxEnt) algorithm (Phillips et al. 2006) in the R: KUENM package (Cobos et al. 2019). The KUENM package allows testing many combinations of features with different regularization multipliers to find the best set of parameters, improving the quality of predictions for SDMs (Steele and Werndl 2013; Cobos et al. 2019). Since MaxEnt requires the delimitation of a calibration area (M *sensu* Soberón and Peterson 2005), we defined its extent following the accessible-area approach (Soberón and Peterson 2005; Rojas-Soto et al. 2024) by identifying the intersection between biogeographic provinces (Morrone et al. 2017) and the world's ecoregions (Dinerstein et al. 2017) that contain at least

Table 1. Endemic-bird species considered in this study. Degree of species specialization to Tropical dry forest (**TDF-S**), and forest dependency (**FD**): 3 = high, 2 = medium, 1 = low; Sensitivity to disturbance (**Snts**): h = high, m = medium, l = low; **Feeding guild**: c = carnivores, f = frugivores, g = granivores, i = insectivores, n = nectarivores.

Family	Species	TDF-S	FD	Snts	Feeding Guild
Cracidae	*Ortalis poliocephala*	3	2	l	f
Odontophoridae	*Philortyx fasciatus*	2	1	l	g
Cuculidae	*Piaya mexicana*	2	2	l	i
Apodidae	*Streptoprocne semicollaris*	2	2	l	i
Trochilidae	*Calothorax pulcher*	1	2	m	n
	Phaeoptila sordida	2	2	l	n
	Cynanthus auriceps	2	1	l	n
	Ramosomyia viridifrons	1	1	m	n
	Saucerottia beryllina	2	2	m	n
Strigidae	*Megascops seductus*	2	3	m	i,c
	Glaucidium griscomi	3	2	m	i,c
Trogonidae	*Trogon citreolus*	3	1	l	f,i
Picidae	*Melanerpes chrysogenys*	2	1	l	i
	Melanerpes hypopolius	1	1	l	f
Tityridae	*Pachyramphus uropygialis*	1	2	m	i
Tyrannidae	*Xenotriccus mexicanus*	1	2	m	i
Grallariidae	*Grallaria ochraceiventris*	1	3	h	i
Furnariidae	*Lepidocolaptes leucogaster*	2	3	m	i
Vireonidae	*Vireo hypochryseus*	3	2	m	i
Troglodytidae	*Pheugopedius felix*	2	2	l	i
	Thryophilus sinaloa	3	2	l	i
Mimidae	*Melanotis caerulescens*	2	1	m	i,f
Turdidae	*Catharus occidentalis*	1	2	m	i,f
	Turdus rufopalliatus	2	1	l	f
	Turdus assimilis	2	3	m	f,i
Passerellidae	*Peucaea humeralis*	2	2	m	i
	Peucaea acuminata	1	1	l	g
	Melozone kieneri	2	2	l	g
Cardinalidae	*Passerina leclancherii*	2	1	l	g
Thraupidae	*Sporophila torqueola*	1	1	l	g

one record of the target species. Furthermore, in cases where the intersection of ecoregions and biogeographic provinces extended significantly beyond the last species' record, we incorporated relevant physical factors that could potentially act as barriers to species dispersal (e.g., Tehuantepec Isthmus; Barve et al. 2011). We downloaded all species records from the Global Biodiversity Information Facility (GBIF: Suppl. material 1). The climatic variables used were those published by Cuervo-Robayo et al. (2014), composed of 19 climatic layers at a spatial resolution of 30 seconds (~1 km^2) derived from precipitation and temperature variables. We selected only variables with Pearson correlation (r) value < 0.80 for each species.

We evaluated model performance by calculating the Area Under the Curve (AUC) (Elith et al. 2011), as well as by applying partial Receiver Operating Characteristic Curves (pROC) via AUC ratio, and Akaike's Information Criterion (AIC) calculated as part of the modeling process in the KUENM package. Evaluation parameters were resampled: 50% of random points with 1,000 data iterations. Afterwards, we ranked the observed AUC ratio with pseudo-replicate values, following the proposal of Peterson et al. (2008). Once all SDMs were created, we used the 10-percentile training presence threshold to make binary presence-absence maps. This threshold identifies suitable pixels that are predicted to have similar suitability as those that contain the species occurrence record and rejects 10% of the records with the lowest suitability to minimize over-prediction caused by possible outliers in each species database. We constructed the species richness map by summing the species' model maps to the pixel level with the raster calculator tool in QGIS (QGIS Development Team 2020).

Land use, land cover, and connectivity index

We used vector layers of land use and vegetation cover Series V (INEGI 2013) and Series VII (INEGI 2018) from the National Institute of Statistics and Geography (acronym INEGI in Spanish), both at a scale of 1:250,000. Series V and VII were selected due to their highly comparable methodologies, which reduces potential bias. INEGI's vegetation covers are derived from the interpretation of Geomedian images from the LANDSAT satellite and a field validation carried out by the INEGI before publication. INEGI has developed a methodology to classify vegetation types according to Rzedowski (2006), considering ecological, floristic, and physiognomic characteristics. Vegetation types are also classified into "primary" and "secondary" through an evaluation of the physiognomic characteristics, using a successional framework that considers criteria such as canopy height, leaf cover, compositional diversity, and the prevalence of certain species (using field verifications). "Primary vegetation" is defined by INEGI (2013) as vegetation that remains or appears unaltered, while "Secondary vegetation" refers to a type of primary vegetation that has been removed or altered by various human or natural factors. There are probably no primary forests in the Americas, so we refer to INEGI's "primary" classification as "old-growth". This systematic approach enables a detailed analysis of vegetative patterns, leading to a better understanding of biodiversity and ecosystem stratification. By applying these technical parameters, INEGI's field verifications offer a mechanism for empirical vegetation categorization. To manage the large number of natural vegetation types and land-use classes, we classified them into fewer categories to make them easier to manage. We reclassified all coverage corresponding to Tropical Dry Forest types (e.g., low deciduous, low sub-deciduous, medium sub-deciduous forest; INEGI 2015; Suppl. material 2). These were further labeled into two classes: old-growth and secondary forests, using QGIS (QGIS Development Team, 2020).

To estimate connectivity between TDFs patches in the BBBP, we used the "Conefor Sensinode 2.6" program (Saura and Torné 2009). We calculated the Integral Index of connectivity (IIC) for each of the two time periods of the INEGI coverage (2013 and 2018). The IIC is calculated by considering the size, shape, and spatial arrangement of these patches, providing a numerical value

that reflects the overall connectivity and accessibility across the landscape; it ranges from 0 to 1 and increases with improved connectivity (Pascual-Hortal and Saura 2006). Although species respond individually and differently to ecosystem fragmentation (Liu et al. 2018), it is common to adjust and estimate a connectivity index for all study subjects to measure the effects on species richness (Saura 2013). Therefore, the connectivity index was calculated for TDFs, taking a dispersal constant of 1,000 m to the nearest edge of the forest patch, which allows the estimation of the overall connectivity value between vegetation patches (Nathan 2006; Borda-Niño et al. 2017). Then, we defined intervals according to the IIC values, including a) very high, b) high, c) moderate, d) low, and e) very low, determined by the Jenks natural breaks process to estimate the changes that occurred in the IIC scale for the TDFs in the BBBP in the two dates, corresponding to INEGI's Series V (2013) and Series VII (2018). We used the TerrSet environment to estimate the losses, gains, total changes, and exchanges between connectivity classes (Clarklabs 2020).

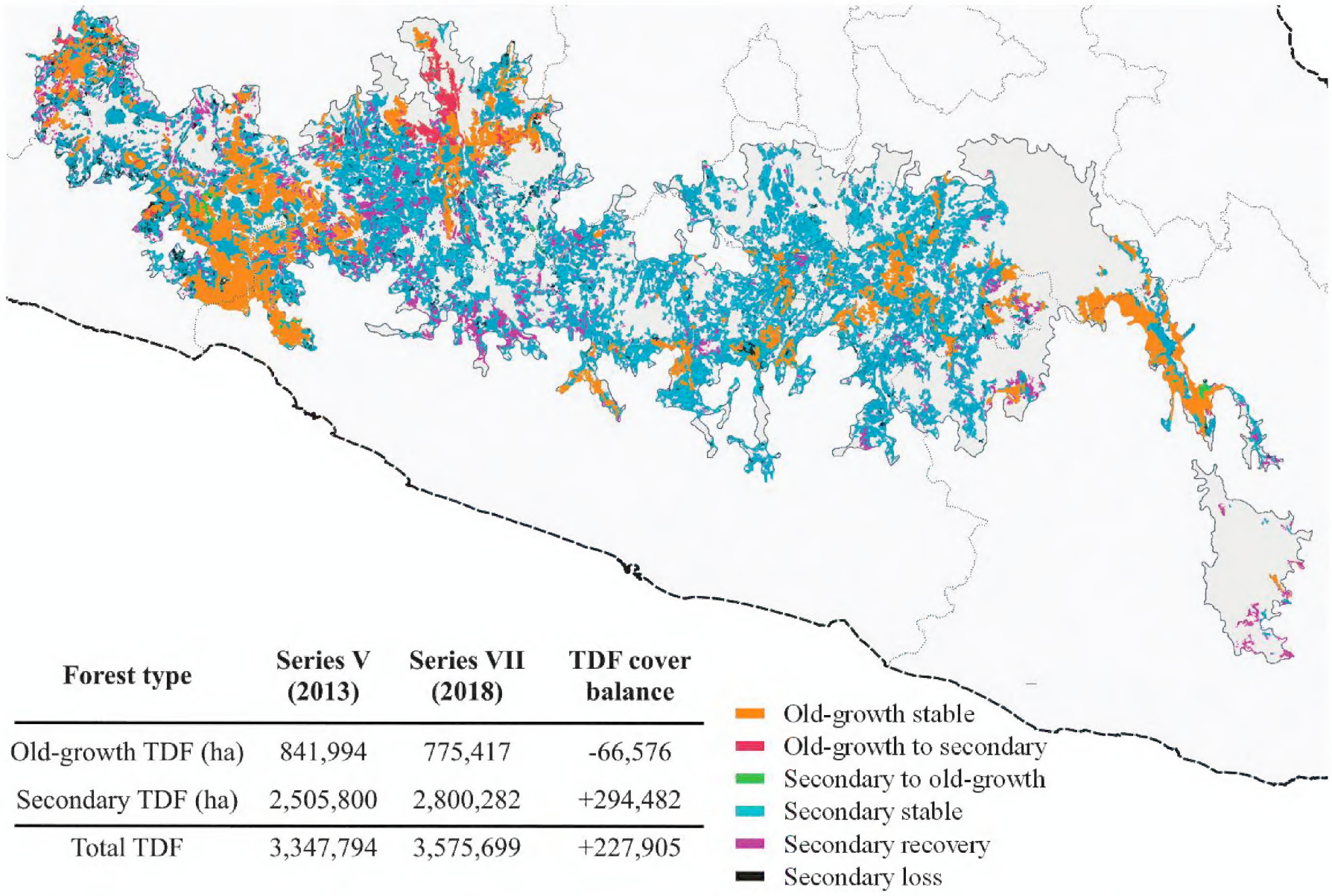
Impact assessment of connectivity change in tropical dry forests for species distributions and priority areas

To identify the impact of connectivity changes over time, we quantified three different features: 1) the connectivity variation between old-growth and secondary forest covers, 2) the connectivity shifts impacting the distribution of each bird species and the overall bird richness, and 3) the connectivity alterations within PAs and IBAs (Arizmendi and Márquez 2000; Devenish et al. 2009, CONANP 2022). Using Boolean Algebra and spatial statistical tools (QGIS), we determined the affected areas for each species and the proportion of their range within each connectivity class. Finally, we assessed the impact on PAs and IBAs by overlaying their polygons on the IIC map to quantify the area affected by connectivity loss.

Results

Within the study area, TDFs experienced an increase from 44% to 47%, which represents a net expansion of 227,905 ha between 2013 and 2018 (Fig. 2). We found a noticeable shift in forest composition, characterized by an increase in secondary forests and a reduction in old-growth TDFs in the BBBP. The west-central and easternmost regions of the BBBP concentrated the main transitions from secondary to forests with characteristics of TDFs old-growth forests.

In 2013, most TDFs within the study area were classified in the lower-connectivity classes, covering a significant portion of the total area (Table 2). In contrast, the areas with the highest connectivity classes, "high" and "very high", accounted for a smaller fraction of the total TDFs. In 2018, there was a decline in the old-growth forest that resulted in the reduction of the TDFs in the "very high" and "high" connectivity classes, equivalent to 7,512 ha, and 103,000 ha, respectively. Nevertheless, when considering both old-growth and secondary forests, there was an overall increase in the "very high" class and a decrease in the "high" class. In contrast, secondary-forest cover gained almost 100,000 ha in its lowest class (very low; Table 2).



Forest type	Series V (2013)	Series VII (2018)	TDF cover balance
Old-growth TDF (ha)	841,994	775,417	-66,576
Secondary TDF (ha)	2,505,800	2,800,282	+294,482
Total TDF	3,347,794	3,575,699	+227,905

Figure 2. Old-growth and secondary tropical dry forests (TDF) dynamics based on INEGI (2013, 2018) in the Balsas Basin Biogeographic Province.

Table 2. Tropical dry forests (TDFs) area per connectivity class. We present the type of forest cover, years, connectivity class in ha, and the percentage shown in parentheses.

Forest type	Year	Connectivity class				
		Very High	High	Moderate	Low	Very Low
Old-growth	2013	194,747 (6)	144,665 (4)	57,099 (2)	113,539 (3)	331,945 (10)
	2018	187,235 (5)	41,529 (1)	153,384 (5)	131,422 (4)	261,848 (7)
Secondary	2013	371,907 (11)	58,758 (2)	215,823 (6)	803,335 (24)	1,055,976 (32)
	2018	452,725 (13)	70,662 (2)	409,067 (11)	713,312 (20)	1,154,516 (32)
Total	2013	566,654 (17)	203,423 (6)	272,922 (8)	916,874 (27)	1,387,921 (42)
	2018	639,960 (17)	112,191 (3)	562,451 (16)	844,734 (24)	1,416,364 (40)

In 2013, forest fragments in the western and central regions of the BBBP had higher connectivity than the rest of the TDFs in the study area, which had “moderate” to “very low” connectivity (Fig. 3). However, by 2018, there was a decrease in connectivity values in the western region of the BBBP, especially in the state of Michoacán where secondary forests declined from “very high” to “moderate”, while "high" connectivity persisted consistently in Guerrero State throughout the study period. The areas in the states of Guerrero and Michoacán with “high” connectivity remained along the borders of the Sierra Madre del Sur Mountain system in the southwestern section of the study area. It is important to note that the increase in connectivity pertained specifically to secondary forests. In contrast, the decrease in connectivity in Michoacán is more generalized and encompasses both old-growth and secondary TDFs.

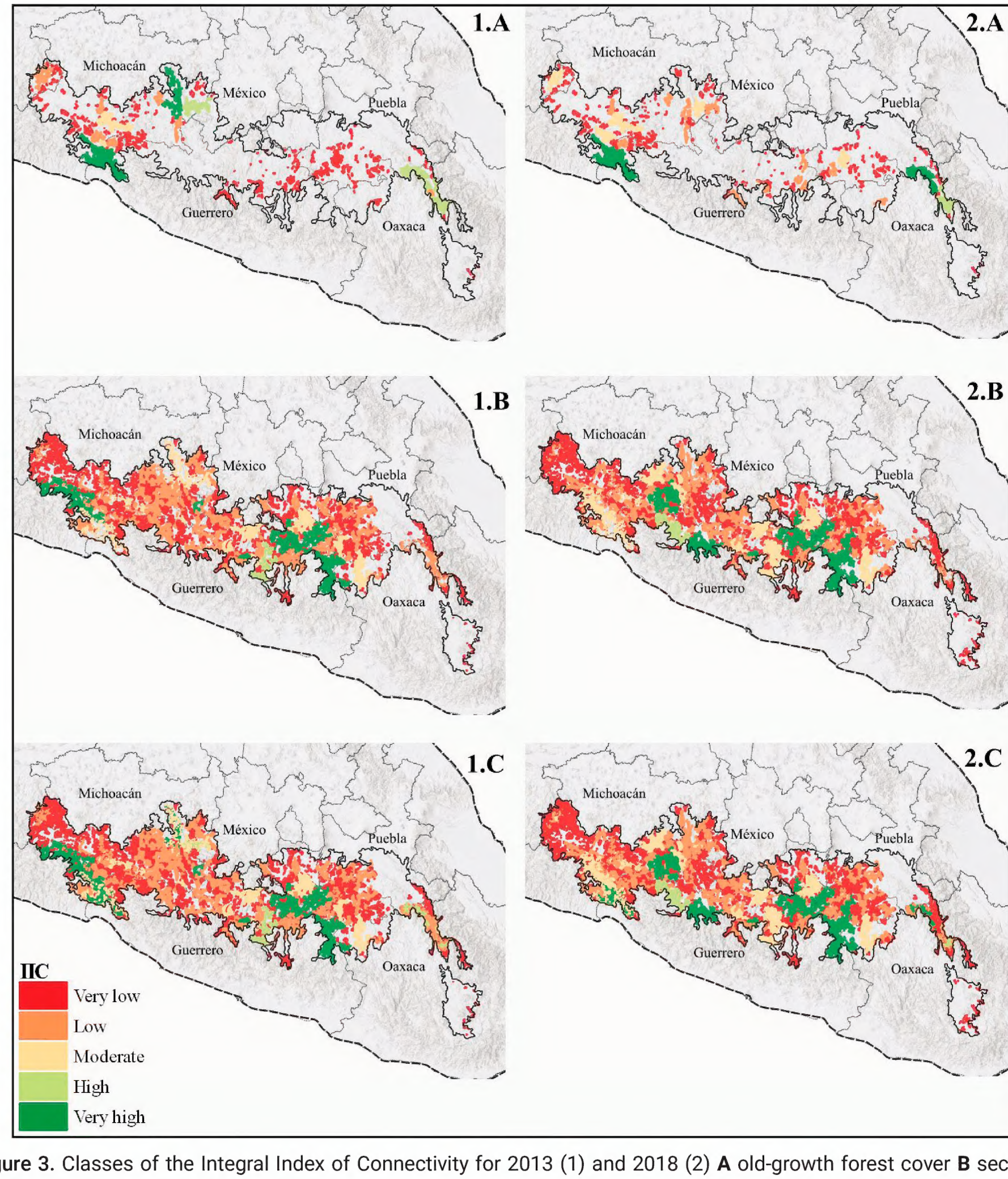


Figure 3. Classes of the Integral Index of Connectivity for 2013 (1) and 2018 (2) **A** old-growth forest cover **B** secondary-forest cover **C** overall TDF cover.

Comparison of the distribution map of the analyzed bird species with the TDF-cover dynamics (including loss, gain, and stable covers), showed that only three of the thirty species in this study (*Sporophila torqueola*, *Turdus assimilis*, *Vireo hypochryseus*) decreased total forest cover within their distribution areas between 2013 and 2018, but, the variation in connectivity change within the range of each species was closely linked to their reliance on old-growth or secondary-forest cover (Suppl. material 3). The expansion of secondary forest occurred predominantly in specific connectivity categories, with 27 species experiencing this growth within connectivity category “very low”, 21 species within connectivity category “moderate”, and 18 species within connectivity category

"very high" (Table 3). Surprisingly, 16 species showed a simultaneous increase in both extreme levels of connectivity (very high and very low), of which 14 species demonstrated a more substantial increase in the "very low" connectivity category than "moderate" (e.g., Fig. 4, for all species, see Suppl. material 3). However, the expansion of secondary forest increases the distribution area for some species. The places where this increase occurred were predominantly associated with connectivity classes "low" and "very low" (see Table 3).

According to the endemic-bird-richness map (Fig. 5), the areas where 26 species are potentially distributed are on the borders of the BBBP alongside the mountain complexes in Michoacán and México States, as well as in the central area of Puebla, Morelos, and Guerrero States. Additionally, some regions with significant levels of endemic-species richness were not included in conservation instruments such as PAs (actually protected spaces) or in suggested areas that are worth preserving, such as IBAs (Fig. 5c). Only 12% of TDF fragments in the BBBP were located in designated protected areas under national conservation categories. In contrast, if all the IBAs were protected, 17% of the TDFs within the study area would be in PAs.

We recorded an increase of 3,000 ha of TDFs inside PAs from 2013 to 2018. However, there are many changes in the forest dynamics inside PAs. We observed an increase of 27,723 ha in areas with "very high" connectivity. The area expanded from 79,098 ha in 2013 to 106,821 ha in 2018. This growth was particularly noticeable in old-growth forests, which experienced an increase of 59,163 ha (Table 4). In contrast, secondary forests in the same connectivity class experienced a substantial decrease of 31,525 ha. Additionally, moderate and very-low connectivity classes tended to increase their area over time in PAs and IBAs (Table 4). On the other hand, areas classified as "high" connectivity experienced a marked decrease inside these priority areas.

Table 3. Number of species that increased, remained stable, or decreased their distribution range within the different connectivity classes in the Tropical Dry Forests (TDFs) of the Balsas Basin Biogeographic Province from 2013 to 2018.

Connectivity class	TDF cover	Increase	Persistence	Decrease
Very high	Old-growth	9	4	17
	Secondary	20	0	10
	Total	18	0	12
High	Old-growth	2	15	13
	Secondary	7	2	21
	Total	7	2	21
Moderate	Old-growth	0	1	29
	Secondary	27	1	2
	Total	21	2	7
Low	Old-growth	23	1	6
	Secondary	5	0	25
	Total	7	0	23
Very low	Old-growth	20	0	10
	Secondary	26	0	4
	Total	27	0	3

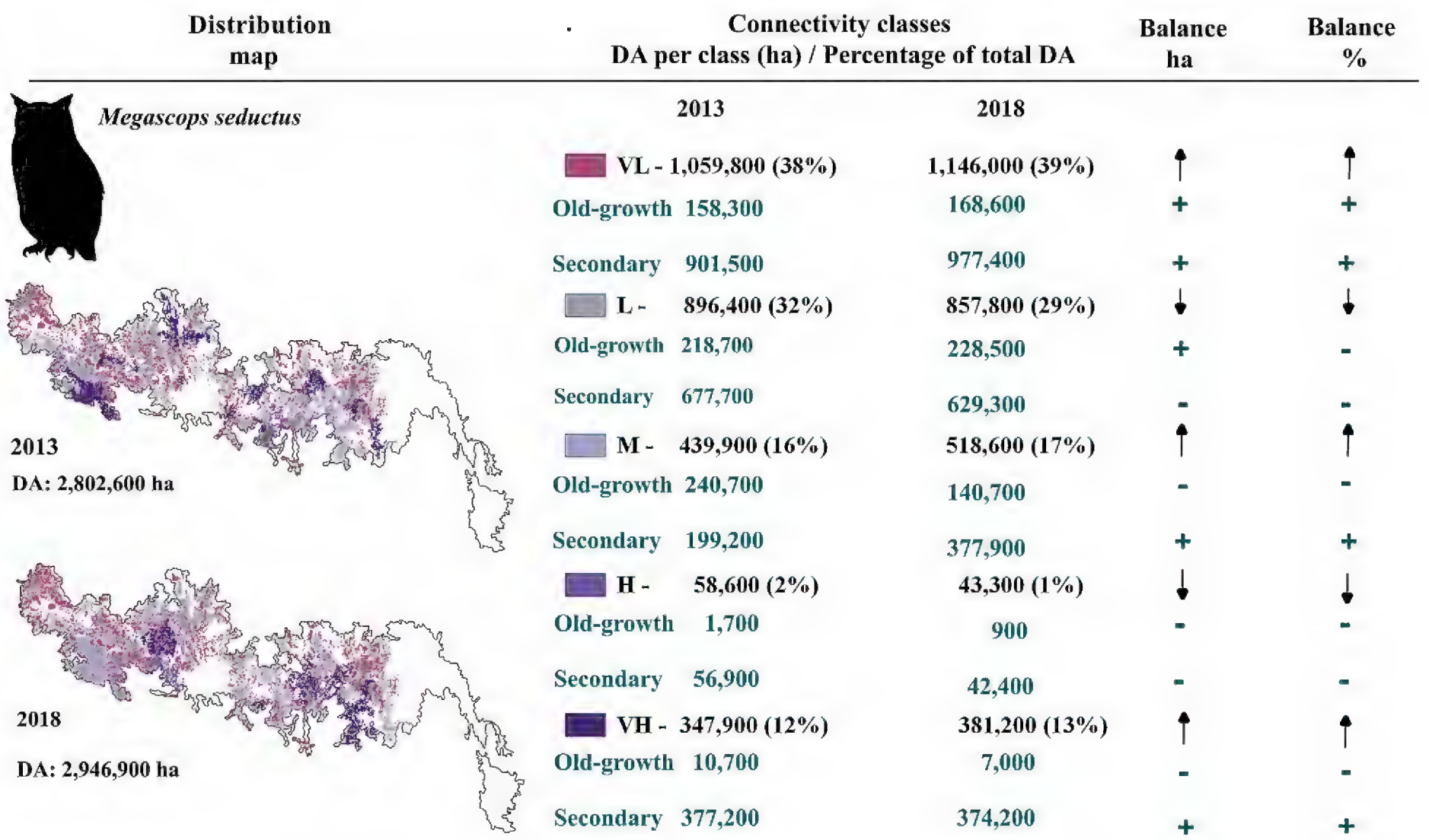


Figure 4. Example of net change in species distribution area (DA) and percentage of DA for each connectivity class. Connectivity classes are very low (VL), low (L), moderate (M), high (H), and very high (VH). The effect of the change was classified as positive (+), and negative (-) for each forest cover type and overall connectivity.

Table 4. Dynamics of the tropical dry forests (TDFs) cover inside protected areas (PAs), and in the important bird areas (IBAs). We give the connectivity class, TDF cover type: old-growth, secondary, and both (Total), and the extent (ha) for 2013, 2018 and the balance from 2013 – 2018 in the Balsas Basin Biogeographic Province.

Connectivity Class	Forest cover type	PAs (ha)			IBAs (ha)		
		2013	2018	Balance	2013	2018	Balance
Very high	**Total**	**79,098**	**106,821**	**27,723**	**94,447**	**130,307**	**35,860**
	Old-growth	42,026	101,275	59,249	20,214	79,719	59,505
	Secondary	37,072	5,546	-31,525	74,233	50,588	-23,645
High	**Total**	**95,370**	**36,207**	**-59,163**	**102,122**	**39,221**	**-62,901**
	Old-growth	95,370	36,207	-59,163	97,143	39,221	-57,922
	Secondary	–	–	–	4,979	–	-4,979
Moderate	**Total**	**75,808**	**127,601**	**51,793**	**76,417**	**136,556**	**60,139**
	Old-growth	52,510	77,811	25,300	21,560	40,249	18,689
	Secondary	23,298	49,790	26,492	54,857	96,307	41,450
Low	**Total**	**75,949**	**35,530**	**-40,419**	**111,369**	**88,501**	**-22,869**
	Old-growth	30,305	6,583	-23,723	29,061	20,132	-8,930
	Secondary	45,643	28,947	-16,696	82,308	68,369	-13,939
Very low	**Total**	**98,536**	**121,807**	**23,271**	**196,529**	**198,241**	**1,712**
	Old-growth	27,200	31,633	4,433	49,888	46,321	-3,567
	Secondary	71,336	90,175	18,838	146,641	151,920	5,279

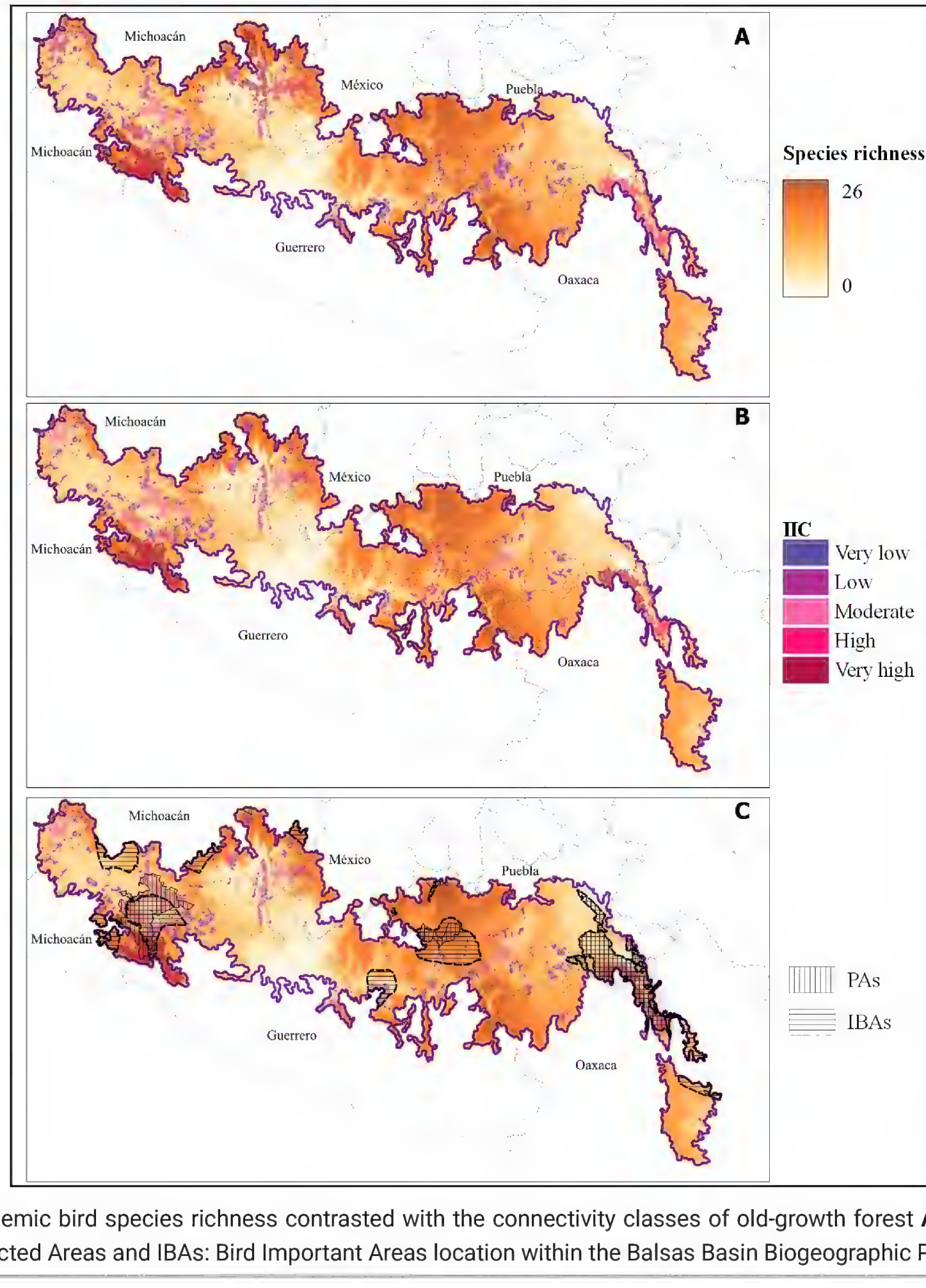


Figure 5. Endemic bird species richness contrasted with the connectivity classes of old-growth forest **A** 2013 **B** 2018 **C.** PAs: Protected Areas and IBAs: Bird Important Areas location within the Balsas Basin Biogeographic Province.

Discussion

In this study, we found evident changes in old-growth and secondary tropical dry forests (TDFs), especially in the north-central BBBP. Concurrently, there was an increase in secondary forests throughout the study area (Fig. 2). Nonetheless, it is important to recognize a possible limitation due to INEGI's definition of primary (old-growth) and secondary forests (2013, 2018). Particularly, within transition zones from primary (old-growth) to secondary TDFs, two scenarios might occur: 1) old-growth forests are changed to other land-use and subsequently are abandoned and initiate a regeneration process, transforming into secondary forests, and 2) areas categorized as secondary forest could be derived from degraded old-growth forests yet retain a structure similar to secondary forest. Additionally, in regions where we detected increases in old-growth TDF cover, the regeneration

of old-secondary forests produced changes in the structure and composition of both strata and species that mirror a mature forest, leading to the classification of those covers as primary (old-growth). Our results indicate trends aligning with other national and regional studies. For instance, Velázquez et al. (2010) noted a 17% loss of old-growth vegetation in México, with a slight recovery of 1.5% through revegetation. Rosete-Vergés et al. (2014) recorded a 35% annual decrease in old-growth forests transitioning to secondary forests and a 1.5% secondary forest recovery from other land uses, indicating a widespread shift to secondary forests due to land-use and land-cover changes (Corona et al. 2016, FAO 2020b).

Nevertheless, this growth in secondary forests might be a short-term increase since other researchers, such as Rader and Schneider (2022), found alternating patterns of forest loss and modest regrowth in Quintana Roo. Meanwhile, López-Barrera et al. (2014) reported a net increase in dense and sparse forests in Veracruz, which was attributed to reduced agricultural activities. However, these trends were inconsistent in both studies, fluctuating between gains and losses in varying periods, which could indicate a slow and long-term degradation process. These findings underscore the complex and fluctuating nature of forest dynamics, stressing the need to account for temporal variations in forest-cover analyses.

In the BBBP, poorly connected old-growth TDFs predominate; however, the growth of secondary forests and the regeneration of forests with characteristics similar to old-growth forests from secondary patches led to an increase in the area covered with high connectivity in certain regions. In this sense, promoting the maintenance of remaining old-growth forest patches and encouraging passive forest restoration or natural regeneration can improve the overall connectivity of the landscape and mitigate fragmentation effects (Bennet 1990; Fahrig 2003; Mayhew et al. 2019). Our findings support the thesis that secondary forests play a crucial role in providing connections for diverse species, mainly when found near intact old-growth forests (Gray et al. 2007; Chazdon et al. 2009), highlighting the conservation value of secondary forests in mitigating wildlife decline in fragmented landscapes. It is also important to note that this conservation value increases with secondary forest age, as shown by Rocha et al. (2018). The strategy of floristic enrichment in secondary forests by introducing native species from old-growth forests is a promising strategy to improve successional processes. Integrating these species can favor ecological succession from poorly developed secondary to old-growth forests and facilitate the restoration of biodiversity and ecosystem functionality (Ávila-Lovera et al. 2023). This underscores the need for adaptive-management practices that aim to conserve existing old-growth forests and increase the ecological value of secondary forests. Furthermore, it highlights the importance of enacting robust protective measures through legislation.

Bird communities, including a variety o diverse of guilds and forest dependency levels, are influenced in distinct ways by the age of forest succession, structural characteristics, and landscape variables (Almazán-Núñez et al. 2012; Santamaría-Rivero et al. 2016; Mayhew et al. 2019). Granivorous bird species tend to be much more resilient to changes in vegetation structure than frugivorous species. For instance, bird diversity in the BBBP showed distinct habitat preferences aligned with their Feeding traits (Vázquez-Reyes et al. 2017). The granivorous species *Peucaea humeralis*, *Passerina leclancherii*, and *Philortyx fasciatus* were more frequently observed in secondary TDFs, this may occur because clearing old-growth forests can promote the development of shrubby and herbaceous

layers prolific in seed production. The studied bird species exhibited diverse distribution patterns, with some showing potential distribution in poorly connected areas. In contrast, other species were predicted to be more common in zones of higher connectivity, reflecting a complex relationship between the level of connectivity of forest cover and bird distributions. Understanding these dynamics is crucial to identify trends that may compromise the conservation of endemic or priority species in the BBBP and other biodiversity-rich regions. For instance, *Megascops seductus* (Fig. 4), an endemic species to the BBBP, inhabits conserved and disturbed TDFs and agricultural landscapes. However, its population density is significantly greater in old-growth forests than in disturbed regions (Alba-Zúñiga et al. 2009). Consequently, the observed decline in connectivity in old-growth TDFs and the rise in areas with reduced connectivity in secondary TDFs may impact *Megascops seductus* and at least 18 other species that, even if they can occur in secondary TDFs, rely on highly conserved places for food, shelter, and breeding (Thompson et al. 2017). The variability in species prevalence across different connectivity areas underscores the urgency for conservation strategies that recognize the intricate dynamics of species-ecosystem interactions and landscape history in conservation planning (Metzger et al. 2009).

The effectiveness of the Protected areas (PAs) network largely depends on its ability to address the connectivity and dispersal requirements of a diverse range of species (Crooks and Sanjayan 2006). Mexican PAs adhere to political and social frameworks that allow specific human activities and regulate resource extraction with an emphasis on sustainable development and the well-being of local communities (DOF 2022), which, as in other countries, have sparked debates regarding its effectiveness in preserving the ecological integrity of PAs (Miller et al. 2011; Shafer 2015). The increase in old-growth vegetation and the expansion of well-connected TDFs within PAs indicate forest maturation, suggesting that this protection model can contribute to successful conservation efforts in the BBBP. It is necessary to reinforce the management strategies within and around the PA network, allowing the maintenance of successional processes from secondary to old-growth forest (Rocha et al. 2018; Mayhew et al. 2019; Acevedo et al. 2023). This is especially important because of the global conservation priority of TDFs, and their current under-protection and limited representation within existing PAs in the study area (Miles et al. 2006; Portillo-Quintero and Sánchez-Azofeifa 2010; Prieto-Torres et al. 2016). Despite the increases in TDFs within PAs in the BBBP, it is crucial to recognize that TDFs are predominantly in the lower-connectivity classes. This could potentially lead to the isolation of species, particularly those with limited dispersal capabilities (Fahrig 2003; Haddad et al. 2003). Although direct data on the mobility of our studied species is lacking, literature on closely related species suggests that many of them might have large home ranges and greater mobility, which could facilitate connectivity over the 1,000-meter threshold used in this study. For instance, while species with low movement ability, such as quails, tend to have small home ranges, typically ranging between 2–9 hectares (Franco et al. 2006), they tend to be more resilient to disturbed habitats due to their ability to use resources in altered environments, thus enabling them to move between secondary TDFs. In contrast, owl species tend to exhibit larger home ranges that can exceed 1,000 hectares (Carey et al. 1990), but often rely on extensive old-growth forests which can limit movements between poorly connected forests. This observation reinforces the

significance of connectivity in conservation strategies and underlines the need for comprehensive management approaches. Such approaches should address these spatial dynamics to prevent the fragmentation and isolation of essential habitats (Crooks and Sanjayan 2006).

Some IBAs may play a crucial role in expanding the PA network and are significant to bird conservation efforts (Arizmendi and Márquez 2000; Devenish et al. 2009). If all IBAs were in the protected area system, the BBBP would have a significantly larger area covered by highly connected TDFs under protection (17% instead of 12%), contributing to international conservation targets (IPBES 2019, CBD 2020). The International Union for Conservation of Nature (IUCN) highlights the importance of incorporating all areas identified as priority areas in terms of ecosystems, species, and resources in PA systems, or to establish initiatives with landowners, government entities, or civil associations to contribute to practical conservation actions (Borrini-Feyerabend et al. 2013; Vimal et al. 2021). Understanding how bird species interact with forest connectivity is critical to develop targeted conservation strategies, allowing the allocation of the limited conservation resources to priority areas (such as IBAs), especially those at lower altitudes which are more susceptible to unsustainable uses, is crucial for effective conservation strategies in the study region.

Conclusions

Tropical dry forests of the BBBP showed changes in their structural connectivity between 2013 and 2018. The old-growth forests in the study area have lost 8% of their original cover; conversely, the coverage of secondary forests has increased by 10%. Also, our results revealed a landscape of changing forest connectivity within the BBBP and its implications for endemic bird species. In some cases, the increase in secondary forests favored connectivity among patches of old-growth forest and thus may reduce the potential adverse effects on bird populations. However, differences in landscape connectivity remain a challenge in maintaining biodiversity. Adaptive management practices may be needed to maintain connectivity and increase the quality of secondary forests for species dependent on tree species typical of old-growth forests.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: ORS, FJSS, AGC. Data curation: AGC. Formal analysis: FJSS, AGC, FLB. Investigation: AGC, FLB, ORS. Methodology: FLB, ORS, AGC, FJSS. Supervision: ORS, FJSS. Validation: FJSS, AGC. Visualization: AGC. Writing - original draft: AGC, ORS, FJSS. Writing - review and editing: FLB.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

Supplementary material 1

Information related to the species used as study case

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Supplementary material 2

INEGI's vegetation covers grouped to be included in the Tropical Dry Forest class

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Supplementary material 3

Net change in area and total species range percentage for each connectivity class.

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